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Relationships of the Indian phytosaur *Parasuchus hislopi* Lydekker, 1885

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Abstract: The neotype skull of the Indian phytosaur *Parasuchus hislopi* Lydekker, 1885 (ISI R42) is re-evaluated and compared with the type material of other basal phytosaurs. *Parasuchus hislopi* is extremely similar to species previously placed in *Paleorhinus* (*P. bransoni* and *P. angustifrons*), sharing with them such characters as a series of nodes on the lateral surface of the jugal, paired ridges on the squamosal, and a frontal depression. *Parasuchus hislopi* represents a valid species: it can be distinguished from *P. bransoni* by a relatively low narial eminence and *P. angustifrons* by the absence of paired nasal depressions. Inclusion of *Parasuchus hislopi* in a phylogenetic analysis of phytosaurs recovers it in a well-supported clade with *P. bransoni* and *P.*

angustifrons. *Parasuchus* is considered the senior synonym of *Paleorhinus* and *Arganarhinus*.

Parasuchus (here considered to include *P. hislopi*, *P. angustifrons*, *P. bransoni*, and *P.*

magnoculus) has a broad circum-Pangaeian distribution, with species occurring in the

southwestern United States, Morocco, central Europe, and India. Phytosaur higher-level

taxonomy is also revised: Parasuchidae is redefined to include ‘*Paleorhinus*-grade’ phytosaurs

and the later-diverging Mystriosuchinae (the group formerly known as Phytosauridae), and

Pseudopalatinae is renamed Mystriosuchini for reason of priority.

Key words: Phytosauria, Triassic, India, biogeography, phylogeny

Running headline: INDIAN PHYTOSAUR *PARASUCHUS*

PHYTOSAURS are a species-rich but morphologically conservative group of carnivorous archosauriforms known almost exclusively from Upper Triassic rocks (Stocker and Butler 2013). Although broadly distributed, phytosaurs are only common components of continental tetrapod assemblages in Laurasia. Known Gondwanan phytosaur remains consist primarily of isolated elements, unidentifiable beyond Phytosauria (e.g. Dutuit 1978; Kischlat and Lucas 2003). An exception to this pattern is the Upper Triassic record of India, which has yielded an abundance of phytosaur fossils, including complete skeletons. As is typical for phytosaurs, the Indian specimens have a complicated taxonomic history, but the majority have traditionally been referred to the species *Parasuchus hislopi*.

Lydekker (1885) initially named *Parasuchus hislopi* based on a series of skull and skeletal fragments from the Maleri Formation (Pranhita-Godavari Valley, Telangana). Huene (1940) reviewed the Maleri tetrapod material and determined that Lydekker's type series for *P. hislopi* was a chimaera composed of a rhynchosaur basicranium and various phytosaur elements. Abandoning the name *Parasuchus hislopi* (see below), Huene (1940) established a new species name (aff. *Brachysuchus maleriensis*) for the Maleri material, taking as the holotype a large phytosaur snout (GSI 16691) collected by the Geological Survey of India. In a subsequent review of the Maleri fauna, Colbert (1958) referred 'aff. *B. maleriensis*' to an expanded genus *Phytosaurus*. Gregory (1962) considered all the Maleri phytosaur material to be undiagnostic.

Chatterjee (1978) revived use of the name *Parasuchus hislopi* for the Indian phytosaur, and referred extensive new material from the Maleri and Tiki formations to this species. At the core of his redescription was a pair of articulated, associated skeletons (ISI R42 and R43), one of which (ISI R42) is nearly complete. Based on that material, Chatterjee (1978) recognized *P. hislopi* as a valid species of basal phytosaur, closely related to *Paleorhinus* from North America

and Europe. However, Hunt and Lucas (1991) and Long and Murry (1995) both followed Gregory (1962) in regarding *Parasuchus hislopi* as a nomen dubium, arguing that Lydekker's (1885) fragmentary type material exhibits no characters that permit confident association with Chatterjee's (1978) specimens. Central to this uncertainty was Huene's (1940) 'aff.

Brachysuchus maleriensis' snout, which appears to represent a different taxon than ISI R42 and R43: unlike Chatterjee's (1978) skulls, which have an extremely elongate, low snout and nares situated completely anterior to the antorbital fenestra (as in *Paleorhinus*), the snout of 'aff. *B. maleriensis*' is relatively tall with posteriorly-positioned nares (as in later-diverging phytosaurs; Long and Murry 1995; Stocker 2010). Hunt and Lucas (1991) referred Chatterjee's (1978) specimens to *Paleorhinus*, a referral followed in subsequent studies (e.g. Heckert and Lucas 1998).

In order to preserve use of the name *Parasuchus hislopi*, Chatterjee (2001) petitioned the International Commission on Zoological Nomenclature (ICZN) to designate the complete skeleton ISI R42 as the neotype of the species, superseding all previous lectotype designations. Prior to this, the identity of the name-bearing type for *P. hislopi* was somewhat uncertain. When Huene (1940, p. 7) recognized that the syntype series of *P. hislopi* was chimaerical, he stated that the rhynchosaur basicranium represented "Lydekker's type" and used this as reason to abandon use of the name *Parasuchus*. If that statement is treated as a lectotype designation, then the name-bearing type of *P. hislopi* would pertain to a rhynchosaur, not a phytosaur. However, Chatterjee (1974, p. 252) argued that Huene's "ambiguous designation" did not explicitly establish a lectotype and was thus invalid. Instead, he designated the partial premaxillary rostrum (GSI H20/11) from Lydekker's (1885) type series as the lectotype, so as to provide definite association of the name *Parasuchus* with a phytosaurian element. This dispute has become moot,

however, as the ICZN ruled in favor of neotypification, making ISI R42 the new name-bearing type of *Parasuchus hislopi* (Opinion 2045).

Despite its newfound nomenclatural importance, the neotype of *Parasuchus hislopi* has received very little study subsequent to Chatterjee's (1978) initial description. Lucas *et al.* (2007) accepted Chatterjee's (1978) proposed synonymy between *Parasuchus* and *Paleorhinus* and included all basal phytosaurs (those with nares completely anterior to the antorbital fenestra) in the genus *Parasuchus*. However, recent work has indicated that *Paleorhinus sensu lato* (*Parasuchus sensu* Lucas *et al.* 2007) represents a grade of species at the base of Phytosauria rather than a monophylum (Stocker 2010, 2013; Butler *et al.* 2014). *Parasuchus hislopi* has never been included in a cladistic analysis of phytosaurs—only as the representative basal phytosaur in broader-scale cladistic analyses of archosauriform relationships (Brusatte *et al.* 2010; Nesbitt 2011). Furthermore, despite being known from a complete skeleton, the validity of the species *P. hislopi* relative to other basal ('*Paleorhinus*-grade') phytosaurs is uncertain: Chatterjee's (1978) diagnosis of *P. hislopi* only differentiated it from the type species of *Paleorhinus*, *P. bransoni*, not the numerous referred species. The resolution of these issues is important from both taxonomic (because *Parasuchus* would have priority over any of the generic names currently in use among basal phytosaurs) and biostratigraphic (because *Parasuchus* has been utilized as an index fossil in the Late Triassic; Lucas *et al.* 2007) standpoints, and is of particular import for understanding phytosaur biogeography (as the only Gondwanan phytosaur known from extensive material).

Here we re-evaluate the neotype of *Parasuchus hislopi* (ISI R42; supplemented by information from the referred specimen ISI R43) and compare it with the available material of other currently recognized '*Paleorhinus*-grade' phytosaurs. Chatterjee's (1978) description of

ISI R42 remains a valuable resource and is largely accurate, so we do not consider it necessary to completely redescribe this specimen. However, we do recognize some significant points of disagreement between our interpretation of the skull and that of Chatterjee (1978), and detail proposed changes where applicable.

Institutional Abbreviations. AMNH FARB, American Museum of Natural History, Fossil Amphibian, Reptile, and Bird Collection, New York, New York, USA; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; GSI, Geological Survey of India, Kolkata, India; ISI, Indian Statistical Institute, Kolkata, India; MU, University of Missouri, Columbia, Missouri, USA; TMM, Jackson School of Geosciences Vertebrate Paleontology Laboratory, University of Texas at Austin, Austin, Texas, USA; TTU P, Texas Tech University, Lubbock, Texas, USA; ZPAL, Instytut Paleobiologii PAN, Warsaw, Poland.

GEOLOGICAL SETTING

The Gondwana deposits of India mark the resumption of sedimentation during the Permian-Carboniferous after a long hiatus since the Proterozoic. These deposits crop out in several isolated basins in peninsular India such as the Pranhita-Godavari, Damodar, Satpura, and Son-Mahanadi basins (Fig. 1). The stratigraphic succession of these basins is traditionally subdivided into lower and upper groups based on the presence of *Glossopteris* or *Ptilophyllum* flora, respectively. The basal part of the Gondwana succession shows uniform lithological features in all the major Indian Gondwana basins, whereas the Upper Gondwana succession differs

considerably between these basins and is defined on the basis of distinctive lithology and physical attributes.

Among the four major basins, *Parasuchus hislopi* has been recovered from two Upper Triassic formations: the Maleri Formation of the Pranhita-Godavari basin and the Tiki Formation of the Rewa basin, one of the sub-basins of the Son-Mahanadi basin. A brief review of the geological setting of the two *Parasuchus*-bearing horizons of India is provided here.

Maleri Formation (Pranhita-Godavari basin)

In the Pranhita-Godavari basin, Gondwana rocks occur as a narrow, rectilinear outcrop trending NNW-SSE and are bordered by Proterozoic and/or Archaean rocks on both sides. The Gondwana succession in this basin is overlain by the Deccan Trap basalt of Cretaceous to Palaeocene age (69–63 Ma). The overall dip of the succession is 5° to 12° NE with a general northward paleocurrent direction. Glacial, glaciomarine, fluvioglacial, fluvial, and lacustrine sediments of 3000 m thickness were deposited in this basin during the Permo-Mesozoic interval (Robinson 1970; Read and Watson 1975; Veevers and Tewari 1995).

In the Pranhita-Godavari basin, the Maleri Formation of the Upper Gondwana group conformably overlies the Bhimaram Formation (Table 1), and is represented by a mudstone-dominated (mud:sand ratio ~75:25), nearly 400m thick fluvial succession deposited under a semi-arid climate (Sarkar 1988). The basal (~100 m) Maleri Formation dominantly consists of red mudstone devoid of any siliciclastic sandbodies and passes upward into a succession comprising alternations of 5–20 m thick mudstone and 3–5 m thick, multi-storeyed, tabular to sheet-bodies of medium to fine quartzose sandstone. The mudstones are dominantly red to

brownish red and have been grouped into two types (Dasgupta and Sarkar 2013). Type I mudstones contain in situ pedogenic features such as calcareous glaebules, gleys and wedge-shaped pedis but lack any primary sedimentary structures like beddings and laminations. Type II mudstones have features like horizontal to low angle inclined parallel laminated heteroliths, ripple cross laminations, nested sets of 10–30 cm deep trough shaped scours and cosets of planar cross beds but do not have any pedogenic features. The sandbodies are multi-storeyed and the storey-fills are divided into two groups (Ghosh and Sarkar 2013). Type I have sharp, planar basal erosional surface displaying an assemblage of sedimentary structures (e.g. plane, parallel, horizontal to low-angle lamination with parting lineation, etc.), whereas Type II storeys have concave upward basal erosional surface comprising dune-scale cross-stratified calcarenite following upward in a fining- and thinning upward sandstone. Massive crudely bedded and cross-bedded calcirudite/calcarenite bodies occur throughout the succession either as lenticular bodies or as 5–30 cm thick discontinuous sheets marking the basal bounding surface of some of the storeys of siliciclastic sandbodies (Dasgupta and Sarkar 2013).

The Maleri Formation is one of the richest storehouses of Indian vertebrate fossils, which occur mainly in the red or brown mudstone. This horizon is divided into a lower part with a Carnian fauna and an upper part with an early Norian fauna (Table 1).

Tiki Formation (Rewa basin)

The Rewa basin is rhombic in shape and relatively long in the ENE-WSW direction; the overall attitude of the basin-fill strata is low-dipping ($\sim 5^\circ$) towards northwest. Chakraborty *et al.* (2003)

considered the Rewa basin to be a fault-controlled subsidence basin. The Upper Gondwana stratigraphy of the Rewa basin comprises a thick conformable and continuous Triassic succession consisting of a basal Pali Formation overlain by the Karki and Tiki formations (Table 1). These sediments are unconformably overlain by the Jurassic Parsora Formation (Mukherjee *et al.* 2012).

The 400 m thick Tiki Formation comprises thick, essentially red-coloured, floodplain mud units with well-developed palaeosol profiles, a subordinate amount of coarse to fine grained, quartzo-feldspathic channel-fill sandstones. Two distinct types of sand bodies are noted in the Tiki Formation: a coarse grained, in places pebbly, ribbon shaped, either isolated or multi-storeyed sandbodies showing internally trough cross-bedded strata with mud clasts arranged along foresets and a fining upward successions. The other sandbodies are fine to very fine grained, well sorted, white sandstones, which are sheet like, multi-storeyed occurring within the red mudstone unit. Profuse burrows which are vertical to subvertical, straight or slightly curved, tubular, non-branching and smooth walled occur in these fine-grained parallel-laminated sandstones (Mukherjee and Ray 2012).

The colour of the Tiki mudstone varies from dark reddish brown to moderate red and very dark red. Pale greenish yellow, pale olive, and greyish-green mudstones are also found. The mudstones have well-developed paleosol horizons showing pedogenic features such as coarse, irregular, subspherical to platy glaebules, tubular, tapering and branching calcareous root casts (rhizocretions), irregular pedogenic cracks and slickensides, and colour mottling. Caliche-derived calcirudite/calcarenite units (*sensu* Sarkar 1988) occur either as multi-storeyed units showing large trough cross bedding or as isolated lenticular bodies within the red mudstone (Mukherjee and Ray 2012).

In addition to unionid bivalve shells and petrified wood, the Tiki Formation has yielded a diverse series of fossil vertebrates (Table 1) (Mukherjee and Ray 2012). On the basis of its faunal assemblage, the Tiki Formation has been correlated with the lower unit of the Maleri Formation of the Pranhita-Godavari basin (Datta 2004) and the Camp Springs member of the Dockum Formation, USA (Datta *et al.* 2004), and a Late Triassic (late Carnian) age has been assigned to this horizon (Mukherjee *et al.* 2012).

SYSTEMATIC PALAEONTOLOGY

ARCHOSAURIFORMES Gauthier, 1986

PHYTOSAURIA Jaeger, 1828

PARASUCHIDAE Lydekker, 1885

PARASUCHUS Lydekker, 1885

1904 *Paleorhinus* Williston, p. 696

1995 *Arganarhinus* Long and Murry, p. 38

Type species. Parasuchus hislopi Lydekker, 1885.

Referred species. Parasuchus bransoni (Williston, 1904); *Parasuchus angustifrons* (Kuhn, 1936); *Parasuchus magnoculus* (Dutuit, 1977).

Diagnosis. A ‘*Paleorhinus*-grade’ phytosaur that can be distinguished from all other members of this group by the presence of an anterior frontal depression, bifurcated lateral ridge on the squamosal, and a row of nodes on the lateral surface of the jugal.

Distribution. Popo Agie Formation, Chugwater Group, Wyoming (Upper Triassic: late Carnian); Colorado City Member, Cooper Canyon Formation, Dockum Group, Texas (Upper Triassic: late Carnian–early Norian); Blasensandstein of the Sandsteinkeuper, laterally equivalent to the Hassberge Formation of the Middle Keuper, Germany (Upper Triassic: late Carnian); Krasiejów assemblage, Middle Keuper, Poland (Upper Triassic: late Carnian); Lower Maleri Formation, Telangana, India (Upper Triassic: late Carnian–early Norian); Tiki Formation, Shadol, India (Upper Triassic: late Carnian–early Norian); Timezgadiouine Formation, Argana Group, Morocco (Upper Triassic: late Carnian–early Norian).

Parasuchus hislopi Lydekker, 1885

Figures 2–13

Neotype. ISI R42, a complete skeleton (Figs 2–8, 14A, F).

Neotype locality. Vicinity of Mutapuram village, Pranhita-Godavari Valley, Telangana, India (Chatterjee 1978).

Neotype horizon. Lower Maleri Formation, Upper Triassic (late Carnian–early Norian).

Referred material. ISI R43, a partial skull (missing the anterior portion of the snout) and skeleton (mostly complete but missing some forelimb elements) found associated with the neotype (Figs 9–12); ISI R44, a partial skull (some elements of which are now lost) from the Tiki Formation, Rewa basin, Shadol District, Madhya Pradesh, India (Fig. 13). These specimens can be referred to *Parasuchus* by the presence of either paired lateral ridges on the squamosal (ISI R43) or a series of nodes on the lateral surface of the jugal (ISI R44) and to *P. hislopi* based on circumnarial morphology (low narial eminence with discrete, rugose posterior rim; absence of nasal depressions). Several additional specimens (ISI R 45, R46, R47, R160, and R161) from the Maleri Formation were referred to this species by Chatterjee (1978). We cannot at present confirm those referrals, either because the specimens do not preserve diagnostic features of *P. hislopi* (ISI R45, R46, and R47 are isolated basicranial elements) or because the specimens were unavailable for study (the skulls ISI R160 and R161).

Diagnosis. A species of *Parasuchus* distinguished from *P. bransoni* by a relatively low narial eminence with a raised, rugose posterior margin of the naris (a ‘narial rim’). Distinguished from *P. angustifrons* by the absence of paired depressions on the anterior portion of the nasals. Tentatively distinguished from *P. magnoculus* by the posterior confluence of the raised margins of the nares.

Emended description

ISI R42 consists of a nearly complete skeleton, which provides important information on the postcranial morphology of basal phytosaurs. Unfortunately, our understanding of

phylogenetically-informative postcranial variation in phytosaurs is in its infancy. Our primary goal in this study is the comparison of *Parasuchus hislopi* with other ‘*Paleorhinus*-grade’ phytosaur taxa, most of which are known only from skull material. As such, here we restrict our discussion to the craniomandibular portion of ISI R42. Although probably nearly complete when discovered, the skull of ISI R42 was very roughly prepared, making accurate delimitations of many cranial sutures impossible (contra Chatterjee 1978). Furthermore, large portions of the occiput and palate, shown as present by Chatterjee (1978:pl. 8), are now missing. Various portions of the skull have been restored in or otherwise obscured by plaster, adding to the uncertainty of the skull as presented. Information on the morphology of some of these portions is available from the specimen ISI R43, however.

The premaxillary tip of ISI R42 forms an expanded terminal rosette as is typical of phytosaurs (Figs 2, 3, 6A). Chatterjee (1978:fig. 3) reconstructed the snout as lacking a distinctly downturned tip, but this does not appear to be the case. A downturned premaxillary tip is the ancestral state for archosauriforms (Nesbitt 2011) and is present in most phytosaurs. The rostrum of ISI R42 is partially reconstructed in plaster, including a long portion of the left premaxilla posterior to the terminal rosette (Fig. 4B), possibly distorting the angle of the snout. Additionally, the terminal rosette is overprepared and the ventral surface of its left side is partially restored in plaster (Fig. 3B). Examination of the more intact right side in lateral view shows that a clear terminal downturn was present (Fig. 5A), as in specimens of other ‘*Paleorhinus*-grade’ phytosaurs (e.g. *P. bransoni*, TMM 31100-101; *Ebrachosuchus neukami*, BSPG 1931 X 501).

Chatterjee (1978:fig. 2) reconstructed the terminal rosette in the snout of *P. hislopi* as bearing only two teeth per side. Although poorly preserved, ISI R42 appears to have alveoli for

four teeth per side (Fig. 6A), as in other ‘*Paleorhinus*-grade’ phytosaurs (Dzik and Sulej 2007; Butler *et al.* 2014). The modified total tooth count in the upper jaw is therefore ~47, instead of Chatterjee’s estimate of 45. As noted by Chatterjee (1978), the tooth row exhibits heterodonty between the relatively narrow anterior alveoli and broad posterior alveoli, with a notable increase in alveolar size posterior to the premaxilla-maxilla contact (based on ISI R43). Medial to the tooth row, well-developed alveolar ridges surround a broad, elongate interpremaxillary fossa (Figs 4B, 6B, 12).

On the lateral surface, ISI R43 clearly shows that a zig-zag contact was present between the premaxilla and maxilla (Fig. 11), differing from the reconstruction shown by Chatterjee (1978:fig. 3). A zig-zag suture between the premaxilla and maxilla laterally is present in all known phytosaur specimens where this region is preserved and is probably synapomorphic for the clade as a whole.

The posterior extent of the premaxilla, and its possible contact with the palatine, is uncertain in ISI R42 because of the fragmentary state of the palate (Fig. 4) and transverse crushing of this region. However, ISI R43 preserves some details of this region. The posterior ends of the premaxillae are covered with plaster in this specimen (Fig. 12). However, the tapering anterior end of the left palatine is preserved, and it is clearly separated from the left premaxilla by a medially expanded shelf of the maxilla, as also occurs in at least some other ‘*Paleorhinus*-grade’ phytosaurs (Stocker 2013; Butler *et al.* 2014). Chatterjee (1978:fig. 2) reconstructed the choanae of *P. hislopi* as being small, narrow openings, placed below the external nares, and with anterior borders formed by the palatines. However, ISI R43 and ISI R44 demonstrate that the choanae were placed further posteriorly, immediately posterior to the external nares, as in other ‘*Paleorhinus*-grade’ phytosaurs, and their anterior borders were very

likely formed by the maxillae (Figs 12, 13B). The very broad palatal exposure of the pterygoid reconstructed by Chatterjee (1978:fig. 2) is also unlikely, and can instead be attributed to the damaged state of the palatines in all known specimens of *P. hislopi*.

Chatterjee (1978:fig. 2) reconstructed the ‘septomaxilla’ of *P. hislopi* as making up the entire internarial bar and the posterior rim of the naris, as was done by Kuhn (1936) for *Paleorhinus angustifrons*. However, Butler *et al.* (2014) argued that this was not likely, and that the internarial bar in *P. angustifrons* probably consists of the nasal fused to the ‘septomaxilla’. The sutural boundaries of the ‘septomaxilla’ in ISI R42 are difficult to delimit, and the internarial bar itself is reconstructed with plaster for most of its length. (Figs 2B, 3B, 5C). The internarial bar of ISI R43 is much better preserved (Fig. 10). Anterior to the external nares, the contacts of the ‘septomaxillae’ with the premaxillae are well-preserved, with median processes of the premaxillae separating the septomaxillae along the midline. Laterally, a ‘septomaxilla’-nasal suture is present, running between the anterior margin of the naris posteriorly and a short posterior process of the premaxilla anteriorly. A ‘septomaxilla’-nasal suture cannot be recognized within the internarial bar. However the bar does narrow very strongly at its (poorly preserved) mid-length, and it is possible that the contact was in this position, as suggested for *P. angustifrons* by Butler *et al.* (2014).

The antorbital fossae are damaged in ISI R42, and the dorsal portion of the right antorbital fenestra is covered in too much plaster to be sure of its construction (Fig. 5C). The left antorbital fenestra clearly shows that the maxillary and lacrimal/jugal fossae do not contact ventrally (Fig. 3). Dorsally, the rim of the left fenestra is broken, with a chunk of bone missing between the two fossae. That said, the fossae are still deep at the point of breakage, with no sign of tapering towards the midpoint as is the case ventrally. The right side of ISI R43 confirms

Chatterjee's (1978:fig. 3) original reconstruction of a dorsal contact between the fossae. The maxilla-jugal suture is preserved in ISI R42 (Fig. 3), and shows that the jugal contributed to the posterior end of the antorbital fenestra's ventral margin as reconstructed by Chatterjee (1978). The lacrimal-jugal suture is only preserved on the left side of the skull, and shows that the jugal also contributed to the ventral margin of the orbit (Fig. 3). Adjacent to the anteroventral corner of the infratemporal fenestra, a small fossa extends onto the lateral surface of the jugal, as in other phytosaurs (e.g. *Ebrachosuchus neukami*, BSPG 1931 X 501; *Rutiodon carolinensis*, AMNH FARB 1). Although the lateral surface of the jugal is very poorly preserved, there is evidence that a row of nodes was present in an identical position to that of *P. angustifrons* and *P. bransoni*. On the right side of the skull, there is a row of at least five slightly raised and poorly preserved nodes (Fig. 5C) extending from the anterior margin of the small fossa adjacent to the infratemporal fenestra and the posteroventral corner of the antorbital fossa. As in *P. angustifrons* (Butler *et al.* 2014), this nodal row is separated by a smooth, gently concave margin from the orbital rim. On the left side of the skull these nodes are more poorly preserved and difficult to distinguish. In ISI R43, the lateral surface of the jugal is poorly preserved on both sides, and the presence of nodes cannot be confirmed, but a set of nodes is clearly present on the right side of ISI R44 (Fig. 13C).

Between the posterior margin of the antorbital fenestra and the anterior margin of the orbit, the dorsal surfaces of the frontals, immediately posterior to the nasal-frontal suture, are strongly depressed (Figs 2, 5C). A similar, but less well-developed frontal depression is present in *P. angustifrons* (Butler *et al.* 2014), although the weaker development of this feature in *P. angustifrons* may reflect dorsoventral compression and overpreparation of the skull. Weak, but distinct, depressions at the anterior edge of the frontal are also present in referred material of *P.*

bransoni (e.g. TMM 31100-101) from Texas. The orbits of ISI R42 are surrounded by well-developed, weakly rugose circumorbital ridges that are most prominent along the anterior and dorsal margins (Figs 2, 5C). A deep, crescentic preorbital depression (sensu Hungerbühler 2002) is present on the prefrontal (Fig. 5C). This feature was identified as autapomorphic for *Mystriosuchus* by Hungerbühler (2002), but is also well developed in *P. bransoni* (TMM 31100-101) and *P. angustifrons* (Butler *et al.* 2014). The interorbital skull roof has a weakly sculptured bone surface (Fig. 2), although this may be due to overpreparation, as this region is more strongly sculptured in ISI R43 (Fig. 9A). Strong sculpturing is present on the surface of the posterior process of the postorbital (Fig. 2). The posterior process of the postorbital is only preserved complete on the left side of the skull, where it is slightly displaced laterally. A facet on the dorsal surface of the squamosal shows that the postorbital had a ‘slot-like’ articulation posteriorly. Laterally, the postorbital bears an anteroposteriorly-oriented ridge that continues on to the squamosal, bifurcating near the origin of the posterior process of the squamosal (Fig. 3). The dorsal surface of the squamosal bears a well-developed depression between its medial and lateral edges (Figs 2, 5B).

The infratemporal fenestra is tall (~1.5 times the height of the orbit: left orbital height 3.2 cm, left fenestra height 5.0 cm, right orbital height 3.5 cm, right fenestra height 5.4 cm) and varies in shape between the two sides of the skull (Figs 3, 5B). The trapezoidal shape present on the left side (illustrated in Chatterjee’s [1978:fig. 3] reconstruction of the skull) is attributable to overpreparation and posterior displacement of the quadrate/quadratojugal, artificially expanding the posteroventral margin of the fenestra posteriorly (Fig. 3B). This region is better preserved on the right side of the skull (now broken off of the main cranium), indicating that the posterior margin of the infratemporal fenestra was only slightly concave and sloped posterodorsally to

anteroventrally (Fig. 5B), as in *P. angustifrons* and *P. bransoni* (Butler *et al.*, 2014). The morphology of the infratemporal fenestra may have been somewhat variable within *P. hislopi*, however, as a morphology similar to the left side of ISI R42 is also present in the better-preserved ISI R43 (Fig. 9C) The quadratojugal is subtriangular in shape. The positions of the sutures with the quadrate and squamosal are visible on the right side, and there is a well-developed, posteriorly-facing quadrate foramen situated between the quadrate and quadratojugal (Figs 5B, 7).

The occiput of ISI R42 is very poorly preserved: most of the posterior faces of the right parietal and left otooccipital are missing, and the posterior face of the left quadrate/quadratojugal complex is covered in plaster (Fig. 7). The occipital condyle and associated basicranium is displaced, being rotated ventrolaterally. The occiput is also incomplete in ISI R43, but the basicranium is in the probable life position, such that the paroccipital processes of the opisthotics are horizontal rather than skewed (Fig. 9D).

Chatterjee (1978) reconstructed the external mandibular fenestra as being anteroposteriorly short. However, the anterior and dorsal margins of the fenestrae are reconstructed in plaster on both sides of ISI R42 (Fig. 8B, C). On the left side, there is the finished border of an opening below the last two tooth positions that represents the actual anterior margin of the fenestra (Fig. 8B). This indicates that the external mandibular fenestra was anteroposteriorly elongate and dorsoventrally shallow, similar to the condition in Polish ‘*Paleorhinus*’ (= *Parasuchus*) specimens (e.g. ZPAL Ab III/112; see Dzik *et al.* 2000; Dzik and Sulej 2007), and extended anteriorly as far as the posterior end of the antorbital fenestra.

Comparisons with other ‘Paleorhinus-grade’ phytosaurs

Eight species of ‘*Paleorhinus*-grade’ phytosaurs are currently recognized as valid (Stocker and Butler 2013; Table 2), four of which (*Francosuchus angustifrons*, *Paleorhinus magnoculus*, *Paleorhinus scurriensis*, and *Ebrachosuchus neukami*) have recently received redescriptions (Fara and Hungerbühler 2000; Stocker 2013; Butler *et al.* 2014). Butler *et al.* (2014) recognized two species of ‘*Paleorhinus sensu stricto*’ that formed a clade to the exclusion of the other phytosaurs in their analysis: *Paleorhinus bransoni* and *Paleorhinus angustifrons*. These species were united by the following two unique synapomorphies: a row of nodular ornamentation on the lateral surface of the jugal and a lateral ridge on the postorbital-squamosal bar that bifurcates into two small ridges on the lateral surface of the squamosal. Butler *et al.* (2014) noted, however, that they were not able to determine the distribution of these characters in all ‘*Paleorhinus*-grade’ phytosaurs. In particular, they left the status of *Parasuchus hislopi* an open question, as they had not personally examined the neotype ISI R42.

Comparisons between *Parasuchus hislopi* and the type species of *Paleorhinus*, *P. bransoni* Williston, 1904, are complicated by the poor state of the latter’s holotype (FMNH UC 632 from the Popo Agie Formation of Wyoming). Recent studies (e.g. Stocker 2010, 2013; Stocker and Butler 2013; Butler *et al.* 2014) have instead relied on well-preserved material from the Dockum Group of Texas, particularly the complete skull TMM 31100-101, to represent the morphology of *P. bransoni* (although the widespread use of such ‘proxy holotypes’ among Triassic archosaur workers has been criticized by Parker [2013]). Those specimens were referred to *P. bransoni* by Hunt and Lucas (1991), and that referral was supported by Long and Murry (1995). However, Hunt and Lucas (1991) utilized a much broader circumscription of both the genus *Paleorhinus* and the species *P. bransoni* than has been supported by recent revisions (e.g.

Stocker 2013), including ‘*Paleorhinus*’ (currently *Wannia*) *scurriensis*, ‘*P.*’ *parvus*, and *Promystriosuchus ehlersi* as junior synonyms of *P. bransoni* (see Table 2). The characters Hunt and Lucas (1991) used to refer the Dockum material to *P. bransoni* are generalized features present in nearly all ‘*Paleorhinus*-grade’ phytosaurs and do not permit specific referral to the type species. That said, our examination of FMNH UC 632 suggests that, despite those issues, Hunt and Lucas’ (1991) referral was correct.

FMNH UC 632 (Fig. 14D) is badly distorted and extensively reconstructed in plaster. It does not preserve any of the characters we consider diagnostic for *Parasuchus* at the genus level. The frontals are crushed, sheared, and partially restored in plaster, making it impossible to tell whether a depression was present. The left squamosal and most of the left jugal are missing. The bone surfaces of the right squamosal and jugal are badly damaged, so the presence of fine surface details like jugal nodes or a bifurcating squamosal ridge cannot be confirmed. However, this specimen exhibits a distinctive narial morphology otherwise known only in the Dockum *P. bransoni* skulls: the narial eminence is elevated posteriorly, such that the posterior edge of the naris forms the apex of a triangle in lateral view and the external narial opening is directed anterodorsally. This eminence is formed by a broadly elevated portion of the nasal posterior to the naris, not a swollen posterior rim of the naris itself (as in *P. hislopi* and *P. angustifrons*; see Fig. 14A, B) or elevation of the entire circumnarial region (as in *Angistorhinus*). This morphology is unique among phytosaurs and can be considered autapomorphic for *P. bransoni*. A complete redescription of *P. bransoni* is pending, but at present, we are confident in using TMM 31100-101 (Fig. 14C) as representative of this species for comparative purposes.

ISI R42 exhibits both a bifurcated ridge on the lateral surface of the squamosal and a row of nodes on the jugal, the two characters Butler *et al.* (2014) considered diagnostic for

Paleorhinus. It also shares distinct frontal and preorbital depressions with *Paleorhinus bransoni* and *P. angustifrons*. The question then arises as to whether *Parasuchus hislopi* is actually diagnosable, or represents an indeterminate representative of *Paleorhinus* sensu Butler *et al.* (2014). Chatterjee (1978) listed five characters distinguishing *Parasuchus hislopi* from *Paleorhinus bransoni*: moderately deep skull (low in *P. bransoni*), orbit directed outwards and upwards (more upwards in *P. bransoni*), post-temporal fenestrae of moderate size (small in *P. bransoni*), teeth weakly heterodont (homodont in *P. bransoni*), and overlapping osteoderms (non-overlapping in *P. bransoni*). All of these characters are problematic, and the first three are probably the result of taphonomic deformation. A relatively low skull, dorsally-directed orbits, and small post-temporal fenestrae are also present in BSPG 1931 X 502, the holotype of *Francosuchus* (= *Paleorhinus* sensu Butler *et al.* 2014) *angustifrons*. BSPG 1931 X 502, FMNH UC 632, and TMM 31100-101 all appear to have suffered from postmortem dorsoventral compression (Butler *et al.* 2014). As a result of this style of deformation, these skulls exhibit a lower (in terms of dorsoventral height relative to width) occiput than they would have had in life. It is likely that this deformation also served to decrease the lateral height of the infratemporal fenestra, squash down the interorbital region to make the orbits face more dorsally, and dorsoventrally compress the post-temporal fenestra. ISI R42 and ISI R43, by contrast, are relatively undistorted, with a ‘boxy’ occiput (sensu Stocker 2010).

In later-diverging phytosaurs, the infratemporal fenestra extends far anteroventrally, completely undercutting the orbit in some taxa (e.g. *Machaeroprotopus*). The anterior extent of the infratemporal fenestra differs between ISI R42 and the previously-discussed *Paleorhinus* material; however, we consider these differences to represent a combination of taphonomic artefact and intraspecific variation instead of phylogenetic signal. In BSPG 1931 X 502 and

TMM 31100-101, the anterior margin of the infratemporal fenestra clearly undercuts the orbit, extending just beyond the posterior orbital margin (Fig. 14B, C). In ISI R42, by contrast, the anterior margin of the infratemporal fenestra and the posterior margin of the orbit are at the same level, without overhang of one above the other (Fig. 3). The same morphology is present in an undistorted Polish specimen, ZPAL AbIII/200 (Dzik *et al.* 2000) that is probably referable to *P. angustifrons* (Butler *et al.* 2014). As such, it is possible that the condition in the other *Paleorhinus* skulls is the result of compression-influenced horizontality of the postorbital bar. However, the infratemporal fenestra also undercuts the orbit in the relatively undistorted ISI R43 (Fig. 9C), suggesting that this character is variable at least within *P. hislopi*. It is also probable that this feature varied ontogenetically: in an enormous skull (estimated length ~1.5 m) from the Popo Agie Formation (FMNH PR 130) that Lucas *et al.* (2007) referred to *Parasuchus* sp., the infratemporal fenestra extends beyond the midpoint of the orbit.

Contra Chatterjee (1978), there is no difference in the degree of heterodonty between ISI R42 and specimens of ‘*Paleorhinus sensu stricto*’. Few tooth crowns are preserved in any of these specimens, but increasing alveolar diameter in the posterior portion of the maxilla indicates that *P. bransoni* and *P. angustifrons* both exhibited ‘simple’ heterodont dentition (Butler *et al.* 2014). Differences in osteoderm morphology between ISI R42 and *Paleorhinus* specimens are currently impossible to evaluate, due to the uncertain morphology of the latter.

Despite the problematic status of previous distinctions between *Parasuchus hislopi* and *Paleorhinus bransoni*, there are a few characters that permit reciprocal diagnosis of these species (and *P. angustifrons*). ISI R42 clearly lacks the broadly elevated narial eminence of *P. bransoni*, instead bearing a swollen, rugose posterior margin of the naris (a morphology shared with *P. angustifrons*). ISI R42 differs from *P. angustifrons* only in the absence of depressions on the

anterior dorsal surface of the nasals (Fig. 14E, F). This is a minor distinction, but appears to be consistent in separating the Indian and central European species: these depressions are present in the same position in BSPG 1931 X 502 and the Polish material (Dzik and Sulej 2007; Butler *et al.* 2014), but are absent in all Indian *Parasuchus* skulls we have examined (ISI R42, R43, and R44).

Paleorhinus magnoculus Dutuit, 1977 is known from a single extremely small (275 mm total length) skull from the Timezgadiouine Formation in the Argana Basin of Morocco. Long and Murry (1995) placed this species in a new genus, *Arganarhinus*, on the basis of its proportionally huge orbits and small antorbital and temporal fenestrae. Fara and Hungerbühler (2000) restudied MNHN-ALM1 and concluded that the specimen represents a juvenile, with its distinctive proportions being the result of its early ontogenetic state rather than of taxonomic importance. Unable to find any non-ontogenetically variable features that permit unique diagnosis of MNHN-ALM1, they concluded that *P. magnoculus* and the genus *Arganarhinus* represent nomina dubia. Lucas *et al.* (2007) agreed with Fara and Hungerbühler that this specimen is a juvenile (albeit taking issue with their taxonomic conclusions on philosophical grounds), as do we. The relatively large orbits, small temporal fenestrae, and short snout of MNHN-ALM1 are all typically juvenile features in amniotes.

Re-examination of MNHN-ALM1 reveals that it possesses all of the autapomorphies we recognize for *Parasuchus* (bifurcated squamosal ridge, row of nodes on lateral surface of jugal, frontal and prefrontal depressions) and should be referred to that genus. It is uncertain whether this specimen represents a distinct species. MNHN-ALM1 differs in narial morphology from the species of *Parasuchus* recognized herein. Like *P. hislopi* and *P. angustifrons*, the nares are situated relatively low and directed dorsally, and have a raised posterior margin. However, in

those species, the raised margins of the nares contact posterior to the nares themselves (Fig. 14E, F). In MNHN-ALM1, the raised margins are separated posteriorly, only contacting near the mid-length of the nares (Fig. 14G). It is possible that this is an ontogenetic difference, with these margins swelling with age and becoming confluent. If so, MNHN-ALM1 could represent a juvenile specimen of *P. hislopi*, as it lacks the nasal depressions characteristic of *P. angustifrons*. In the absence of further information on basal phytosaur ontogeny, however, we take this character at face value and tentatively retain *Parasuchus magnoculus* as a distinct species. Hopefully, additional phytosaur material from the Argana Basin currently under study (N.-E. Jalil, pers. comm., 2014) will resolve this issue.

Ebrachosuchus neukami Kuhn, 1936 was included in the genus *Paleorhinus* by Gregory (1962), a placement followed by Hunt and Lucas (1991) and Long and Murry (1995). This taxon is known from a single, well-preserved skull (BSPG 1931 X 501). Butler *et al.* (2014) thoroughly redescribed this specimen and demonstrated that it is not referable to '*Paleorhinus sensu stricto*', instead being more closely related to phytosaurid (*sensu* Stocker 2010) phytosaurs. The extreme length of the rostrum (greater than 3.8 times that of the orbital/postorbital region) distinguishes this species from *Parasuchus hislopi*, as does the exceptionally high tooth count (>50). The consistent alveolar size in BSPG 1931 X 501 indicates that this taxon did not have maxillary heterodonty as in *Parasuchus hislopi*. BSPG 1931 X 501 exhibits an anteroposteriorly longer infratemporal fenestra than ISI R42 (terminating below the midpoint of the orbit anteriorly), although as for the specimens of '*Paleorhinus sensu stricto*' discussed above there is some uncertainty here related to the probable dorsoventral compaction of this specimen. Unlike *Parasuchus*, the maxillary and lacrimal/jugal antorbital fossae do not contact in BSPG 1931 X 501, and the antorbital fenestra is proportionately smaller. Other features distinguishing

Ebrachosuchus from *Parasuchus* include the presence in *Ebrachosuchus* of shorter and broader external nares that possess a broader internarial septum and are situated further posterior on the skull, the absence of raised posterior margins of the nares, broad transverse expansion of the nasals, relatively weakly developed alveolar ridges, the absence of a jugal node row, absence of a bifurcated ridge on the squamosal, and only a weakly developed depression on the dorsal surface of the squamosals (Butler *et al.* 2014).

‘*Paleorhinus*’ *parvus* Mehl, 1928 is known only from the type specimen (MU 530), a partial skull and skeleton from the Popo Agie Formation of Wyoming. The cranial portions of MU 530 preserve the rostrum, nasal region, and the posterior half of the mandible. MU 530 exhibits the same ‘simple’ form of heterodonty (thin, needle-like teeth anteriorly, increasingly broad, spade-shaped teeth beneath the orbital region) present in *Parasuchus hislopi* and most basal phytosaurs. This specimen exhibits significantly greater deflection of the premaxillary tip than ISI R42, but as discussed above this morphology is probably not natural in the latter. However, MU 530 clearly differs from ISI R42 in the high position of the nares: situated on a tall platform showing a sharp break in slope from the premaxillary rostrum, unlike the relatively low, gradually sloping condition in *Parasuchus hislopi*. Lateral crushing in MU 530 is unlikely to account for this difference; although the nasals of this specimen are broken, the subnarial facial portion of the maxilla is well-preserved and shows that this element at least has greater relative height than that of *Parasuchus hislopi*. Overall, these features give ‘*Paleorhinus*’ *parvus* a more *Angistorhinus*-like profile than other ‘*Paleorhinus*-grade’ species.

The ‘Borden County *Paleorhinus*’ is a large skull (TMM 31213-16) from the Dockum Group of Texas that Gregory (1962) initially suggested represents a distinct species. Long and Murry (1995) later formally described this specimen as the holotype of *Paleorhinus sawini*.

Inclusion of this species in phylogenetic analyses has indicated that it does not form a clade with ‘*Paleorhinus sensu stricto*’ and rather represents a later-diverging taxon (Stocker 2010, 2012; Butler *et al.* 2014). TMM 31213-16 can readily be distinguished from ISI R42 by its strongly convex maxillary alveolar margin, larger infratemporal fenestra, and lack of supraorbital ridges, jugal nodes, paired squamosal ridges, and anterior frontal depression. Although similar in proportional height to that of ISI R42, the infratemporal fenestra in TMM 31213-16 is anteroposteriorly longer, undercutting the orbit to a level near the midpoint. The orbits of TMM 31213-16 are also proportionally smaller than those of ISI R42, although this may be attributable to the significantly greater size of the former specimen. As in *Ebrachosuchus* and later-diverging phytosaurs and unlike *Parasuchus*, the maxillary and lacrimal/jugal antorbital fossae do not contact in ‘*Paleorhinus*’ *sawini*.

Langston (1949) described *Paleorhinus scurriensis* based on TTU P-00539, a partial skull from the base of the Dockum Group in Texas. Hunt and Lucas (1991) considered this species synonymous with *P. bransoni*, a stance followed by Long and Murry (1995). More recently, Stocker (2013) redescribed this specimen, recovered it as the earliest-diverging phytosaur in a phylogenetic analysis, and placed ‘*P.*’ *scurriensis* in the new genus *Wannia*. TTU P-00539 is a highly incomplete skull, but shows two features that permit distinction from *Parasuchus hislopi*: the presence of a well-developed ridge on the lateral surface of the jugal and the lack of any contact between the ‘septomaxillae.’

PHYLOGENETIC ANALYSIS

We coded *Parasuchus hislopi* (based on ISI R42 and R43) into a modified version of the phytosaur character matrix of Stocker (2010) and Butler *et al.* (2014). Two new characters were added, which pertain to the presence of a frontal depression and a swollen narial rim (see Appendix). We did not include *P. magnoculus* in the analysis, pending the description of additional Argana Group phytosaur specimens under study by another research group (N.-E. Jalil, pers. comm., 2014). A parsimony analysis was run in TNT v1.1 (Goloboff *et al.* 2008) using New Technology searching (default settings for sectorial searching, parsimony ratchet, tree drift, and tree fusing) and the constraint that minimum tree length must be recovered at least 20 times. Characters 2, 3, and 14 were treated as ordered, following Butler *et al.* (2014). The archosauriform *Euparkeria capensis* was used as the outgroup. Bootstrap analysis was run in TNT using standard resampling with 10000 replicates, and Bremer support was obtained using the script bremer.run after performing a New Technology search and retaining trees suboptimal by up to 20 steps (Goloboff *et al.* 2008).

Twenty most parsimonious trees of length 123 were recovered (CI=0.561, RI=0.760). The strict consensus topology is identical to that of Butler *et al.* (2014) other than in the addition of *Parasuchus hislopi* (Fig. 15). The strict consensus recovered a clade consisting of *Parasuchus hislopi* and the two species of ‘*Paleorhinus sensu stricto*’ (*P. bransoni* and *P. angustifrons*). This clade is supported by three unambiguous synapomorphies (Character states 23:3, 44:1, and 47:1): the bifurcation of the lateral ridge on the postorbital-squamosal bar into two small ridges on the lateral face of the squamosal, the presence of jugal nodes, and the presence of a frontal depression. Within this clade, *P. hislopi* and *P. angustifrons* are recovered as sister taxa based on a single unambiguous synapomorphy (Character state 48:1): presence of a swollen, rugose narial

rim. The *Parasuchus*/‘*Paleorhinus* sensu stricto’ clade is strongly supported in our analysis, with the highest level of bootstrap support (79) of any clade in Phytosauria.

DISCUSSION

The status of Paleorhinus

Ever since Chatterjee’s (1978) description of intact *Parasuchus* skulls, the possibility that this genus might represent the senior synonym of *Paleorhinus* has been recognized. Chatterjee (1978) did synonymize the two genera, albeit retaining *Paleorhinus* as a valid subgenus. Subsequent use of *Paleorhinus* to refer to basal phytosaurs was predicated on the belief that *Parasuchus hislopi* was a nomen dubium; the Maleri skulls described by Chatterjee have consistently been treated as congeneric with *Paleorhinus* (Hunt and Lucas 1991; Long and Murry 1995). After the neotype was designated for *P. hislopi*, Lucas *et al.* (2007) reverted to use of *Parasuchus* as the senior synonym of *Paleorhinus* (see Table 2). It is only recently, with the advent of a cladistic approach to resolving basal phytosaur taxonomy, that there has been uncertainty over whether to refer the Maleri skulls and *Paleorhinus* spp. to the same genus (i.e. whether these taxa form a clade to the exclusion of other phytosaurs) (Stocker 2013; Butler *et al.* 2014).

Our results provide the first computational cladistic evidence for the synonymy of *Parasuchus* and *Paleorhinus*. *Parasuchus hislopi* and ‘*Paleorhinus* sensu stricto’ (*P. bransoni* and *P. angustifrons*; Butler *et al.* 2014) form a well-supported clade in our analysis and differ only in minor features of the narial region. Given that we recover *P. bransoni* outside of the

clade consisting of *P. hislopi* and *P. angustifrons*, it could be possible to retain the genus *Paleorhinus* to refer only to *P. bransoni*. However, given weak intra-clade support, we believe the recognition of a single genus, *Parasuchus*, is in the best interests of taxonomic stability. This will avoid the potentially confusing situation of having currently untested referred species (primarily *P. magnoculus*, but potentially other species in need of redescription, e.g. *Promystriosuchus ehlersi*) jumping between *Parasuchus* and *Paleorhinus* in subsequent analyses.

Phytosaur higher level taxonomy

The recognition of *Parasuchus hislopi* as a valid, diagnosable taxon also has implications for the use of the associated family name Parasuchidae Lydekker, 1885. Phytosaur higher level taxonomy has a confused history, and a number of family-level taxa have been applied to the group. The earliest available name for a phytosaur family is Phytosauridae Jaeger, 1828. Composition of Phytosauridae has varied extensively: Huene (1915) restricted this family to the group currently known as Pseudopalatinae (minus *Mystriosuchus*), whereas Gregory (1962) included all known phytosaurs in the family. Use of the name Phytosauridae has largely continued in more recent scholarship, albeit with further compositional changes. Doyle and Sues (1995) provided the first phylogenetic definition for Phytosauridae: the last common ancestor of *Angistorhinus*, *Mystriosuchus*, *Nicrosaurus*, *Pseudopalatus*, and *Rutiodon* (thus excluding the ‘*Paleorhinus*-grade’ phytosaurs from Phytosauridae). Stocker (2010) continued to use the name Phytosauridae for this node, albeit redefining it as the last common ancestor of *Angistorhinus*, *Leptosuchus studei* Case and White, 1934, and *Mystriosuchus westphali* Hungerbühler and

Hunt, 2000. This circumscription of Phytosauridae has been retained in the majority of subsequent taxonomic studies of phytosaurs (e.g. Stocker 2012, 2013; Stocker and Butler 2013; Butler *et al.* 2014).

Unfortunately, continued use of the taxon Phytosauridae to refer to this node is not tenable from a nomenclatural standpoint. The name Phytosauridae is inextricably linked to its type genus, *Phytosaurus*. The type species of *Phytosaurus*, *P. cylindricodon* Jaeger, 1828, is based on a set of mandibular fragments that are universally considered undiagnostic at the genus and species level (Stocker and Butler 2013). The argument could be made that regardless of the status of *Phytosaurus* as a nomen dubium, if it exhibits the diagnostic features of the larger clade currently called Phytosauridae, then the latter taxon could be retained. However, the type material of *Phytosaurus cylindricodon* does not exhibit any synapomorphies of Phytosauridae sensu Stocker (2010): it can be identified at best as Phytosauria indet. (based on age and general morphology—these specimens do not actually preserve any of the synapomorphies of Phytosauria recognized by Nesbitt [2011]). As such, the name Phytosauridae cannot be utilized to refer to this clade, and must be considered dubious in and of itself.

The next available family-level name for phytosaurs, Belodontidae Cope, 1871, is also based on a dubious genus (*Belodon* Meyer, 1844) and should not be utilized. This leaves Parasuchidae Lydekker, 1885 as the most senior name anchored to a valid taxon. However, as *Parasuchus* lies outside of Phytosauridae sensu Doyle and Sues (1995) and Stocker (2010), Parasuchidae cannot be used as a direct replacement for the name of that clade. Instead, we propose to revert to an expanded definition for the family-level group in phytosaurs (similar to that of Benton 2004), defining Parasuchidae as the last common ancestor of *Parasuchus hislopi* Lydekker, 1885, *Wannia scurriensis* (Langston, 1949), and *Mystriosuchus planirostris* (Meyer,

1863) and all of its descendants. This approach has extensive historical precedent—despite some exceptions (like the aforementioned work of Huene [1915]), for most of the 20th century phytosaurs were included in a single family, and Chatterjee (1978) previously used the name *Parasuchidae* for this group. At present, our proposed node-based taxon *Parasuchidae* includes all known taxa within the stem-based *Phytosauria*. This taxonomic scheme parallels that of aetosaurs, another species-rich, morphologically conservative Triassic archosauriform group in which a single node-based family (*Stagonolepididae*) contains the majority of recognized diversity in a stem-based clade (*Aetosauria*). Although this change contravenes current prevailing usage, we believe it is the best option to provide long-term taxonomic stability for this group.

For the clade previously known as *Phytosauridae*, we use the earliest available name based on a valid included genus, *Mystriosuchinae* Huene, 1915, here defined as the last common ancestor of *Mystriosuchus planirostris* (Meyer, 1863) and *Angistorhinus grandis* Mehl, 1913 and all of its descendants. This taxon name was most recently used by Long and Murry (1995) as a monotypic subfamily for *Mystriosuchus*, which they believed to be an aberrant, highly derived descendant of *Paleorhinus*. By contrast, Ballew (1989), in the first phylogenetic analysis of phytosaurs, recovered *Mystriosuchus* as a close relative of *Nicrosaurus* and *Pseudopalatus*. Long and Murry (1995) also recognized a group containing the latter two genera, which they named *Pseudopalatinae*. Subsequent analyses (Stocker 2010, 2012, 2013; Butler *et al.* 2014) have consistently supported Ballew's (1989) position for *Mystriosuchus*, and this genus was used as an internal specifier in the phylogenetic definition of *Pseudopalatinae* (Parker and Irmis 2006). As such, *Pseudopalatinae* represents a clear junior synonym of *Mystriosuchinae* von Huene, 1915. Here, we use the name *Mystriosuchini* Huene, 1915 to refer to the clade previously called

Pseudopalatinae, and define it as the last common ancestor of *Mystriosuchus planirostris* (Meyer, 1863), *Nicrosaurus kapffi* (Meyer, 1860), and *Machaeroprotopus buceros* (Cope, 1881) and all of its descendants. This is a node-based taxon using the type species of each currently-recognized (Hungerbühler *et al.* 2013) mystriosuchin (=pseudopalatine) genus as an internal specifier. These taxa have been used as specifiers to retain consistency in composition as much as possible with the traditional ‘Pseudopalatinae’, but follow recommendations for phylogenetic nomenclature in prioritizing the use of type species in definitions. A summary of the proposed changes for phytosaur clade names is presented in Table 3.

Phytosaur biogeography

Here we recognize *Parasuchus* as a distinct clade of basal phytosaurs including at least three species. Although not included in our phylogenetic analysis, *P. magnoculus* almost certainly belongs to this clade as well, as it exhibits all the characters herein considered diagnostic for *Parasuchus*. This clade is distributed broadly across the southwestern United States (Wyoming and Texas), Germany, Poland, Morocco, and India in rocks of probably roughly synchronous age (latest Carnian–early Norian; Dutuit 1977; Chatterjee 1978; Long and Murry 1995; Dzik 2001; Butler *et al.* 2014). Furthermore, in many of these localities, *Parasuchus* coexists with later-diverging, ‘*Angistorhinus*-grade’ phytosaurs. Thus, by the time that the earliest definitive phytosaurs first appear in the fossil record, the group is already circum-Pangaean in distribution and phylogenetically diversified. The early evolution of phytosaurs is almost completely unknown—the clade must stretch back into the Early Triassic (Brusatte *et al.* 2010; Nesbitt *et al.* 2010; Nesbitt 2011), but there are currently no well-supported Early or Middle Triassic

phytosaur records (Hungerbühler 2001; Stocker and Butler 2013). As such, it is uncertain whether the broad distribution of *Parasuchus* represents rapid dispersal within a radiating clade (occurring in *Parasuchus* concurrent with that of *Angistorhinus* and other phytosaurs in the late Carnian-early Norian) or a long-term pattern. Pertinent to this question is the enigmatic taxon *Mesorhinosuchus fraasi*, represented by a single specimen (destroyed in WWII) from supposed Early Triassic (Olenekian, Middle Buntsandstein) rocks in Germany. The original description of this specimen and a published photograph (Jaekel 1910) indicate that this animal was extremely similar to (possibly congeneric with) *Parasuchus*. If so, this would suggest extreme conservatism through much of the Triassic for phytosaurs. Regrettably, little more can be said in the absence of the original specimen, and it has been suggested that the *M. fraasi* type was actually a mistakenly labeled Late Triassic fossil (e.g. Hunt and Lucas 1991).

The distribution of phytosaurs in general and *Parasuchus* in particular suggests that there were minimal geographic barriers against phytosaur dispersal across Pangaea in the Late Triassic. Phytosaurian exclusion from various well-sampled Late Triassic assemblages (e.g. Ischigualasto Formation of Argentina, Santa Maria Formation of Brazil, Elliot Formation of South Africa) is thus more likely to be attributable to climatic barriers, as is also likely to be the case for other Triassic taxa with broad but patchy distributions (e.g. cynodonts, kannemeyeriiforms, procolophonids, metoposaurids) (Whiteside *et al.* 2011; Kammerer *et al.* 2013; Brusatte *et al.* 2015). Brusatte *et al.* (2013) argued that greater aridity in southern Gondwana in the Late Triassic explains the absence of phytosaurs in this region. Where phytosaurs are found outside of their main latitudinal belt, their remains tend to be fragmentary and rare, suggesting that although they may have had a presence in these environments, they were not numerically important components of the fauna. The distinction between total

geographic range and abundances within that range is difficult to extract from an incomplete fossil record, but more information on this topic will be crucial to understanding the complex biogeographic patterns of tetrapods in Triassic Pangaea.

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FIGURE CAPTIONS

FIG. 1. Map showing the locations of Gondwana group-bearing geological basins in India: 1, Pranhita-Godavari Basin; 2, Satpura Basin; 3, Son-Mahanadi Basin; 4, Damodar Basin.

Specimens of *Parasuchus hislopi* are known from the Pranhita-Godavari and Rewa (sub-basin of the Son-Mahanadi) basins. [formatted for column width]

FIG. 2. Neotype skull of *Parasuchus hislopi* Lydekker, 1885 (ISI R42) in dorsal view. A, photograph of specimen. B, interpretive drawing of specimen, with plaster shown in hatching.

Abbreviations: afen, antorbital fenestra; afos, antorbital fossa; cor, circumorbital ridge; fd, frontal depression; itf, infratemporal fenestra; ju, jugal; na, nasal; nar, naris; nr, narial rim; oc, occipital condyle; orb, orbit; pmx, premaxilla; po, postorbital; sq, squamosal; sqd, squamosal depression; stf, supratemporal fenestra; tr, terminal rosette. [formatted for page width]

FIG. 3. Neotype skull of *Parasuchus hislopi* Lydekker, 1885 (ISI R42) in left lateral view. A, photograph of specimen. B, interpretive drawing of specimen, with plaster shown in hatching.

Abbreviations: afen, antorbital fenestra; afos, antorbital fossa; ec, ectopterygoid; fd, frontal depression; itf, infratemporal fenestra; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; nar, naris; orb, orbit; pmx, premaxilla; po, postorbital; prf, prefrontal; q-qj, quadrate-quadratojugal complex; sq, squamosal; sqr, squamosal ridges. [formatted for page width]

FIG. 4. Neotype skull of *Parasuchus hislopi* Lydekker, 1885 (ISI R42) in ventral view. A, photograph of specimen. B, interpretive drawing of specimen, with plaster shown in hatching.

Abbreviations: alr, alveolar ridge; bsp, basisphenoid; bt, basal tuber; fr, ventral face of the frontal; itf, infratemporal fenestra; mx, maxilla; oc, occipital condyle; orb, orbit; pal, palatine; par, paroccipital process of the opisthotic; pmx, premaxilla; pr, prootic; stf, supratemporal fenestra; tr, terminal rosette. [formatted for page width]

FIG. 5. Neotype skull of *Parasuchus hislopi* Lydekker, 1885 (ISI R42), details. A, tip of snout in right lateral view. B, posterior temporal region and occiput in right lateral view; C, orbital and narial region in right lateral view. *Abbreviations:* afen, antorbital fenestra; afos, antorbital fossa; cor, circumorbital ridge; dp, downturned tip of premaxilla; fd, frontal depression; fr, frontal; itf, infratemporal fenestra; jun, jugal nodes; mx, maxilla; na, nasal; nar, naris; nr, narial rim; orb, orbit; pfd, preorbital depression; q, quadrate; qf, quadrate foramen; qj, quadratojugal; sqd, squamosal depression; sqr, squamosal ridge; tr, terminal rosette. [formatted for page width]

FIG. 6. Neotype skull of *Parasuchus hislopi* Lydekker, 1885 (ISI R42), details. A, tip of snout in ventral view. B, snout midlength in ventral view. C, basicranium in ventral view. D, palate.

Abbreviations: alr, alveolar ridge; bt, basal tuber; mx, maxilla; oc, occipital condyle; pal, palatine; par, paroccipital process of the opisthotic; pms, mid-premaxillary suture; pmx, premaxilla; pr, prootic; q, quadrate; trr, tooth root in terminal rosette. [formatted for page width]

FIG. 7. Neotype skull of *Parasuchus hislopi* Lydekker, 1885 (ISI R42), occiput. *Abbreviations:* bt, basal tuber; fm, foramen magnum; oc, occipital condyle; par, paroccipital process of the

opisthotic; q, quadrate; qf, quadrate foramen; qj, quadratojugal; so, supraoccipital; sq, squamosal; sqd, squamosal depression. [formatted for column width]

FIG. 8. Neotype mandible of *Parasuchus hislopi* Lydekker, 1885 (ISI R42). A, mandible in dorsal view. B, posterior end of left mandibular ramus in lateral view. C, detail of posterior end of right mandibular ramus in lateral view. *Abbreviations:* amf, anterior margin of mandibular fenestra; mf, mandibular fenestra. [formatted for page width]

FIG. 9. Referred skull of *Parasuchus hislopi* Lydekker, 1885 (ISI R43), orbito-temporal portion. A, dorsal view (anterior is down). B, ventral view (anterior is down). C, left lateral view. D, occipital view. *Abbreviations:* bt, basal tuber; itf, infratemporal fenestra; oc, occipital condyle; orb, orbit; par, paroccipital process of the opisthotic; porb, postorbital bar; q, quadrate; qf, quadrate foramen; sqd, squamosal depression; sqr, squamosal ridges; stf, supratemporal fenestra. [formatted for page width]

FIG. 10. Referred skull of *Parasuchus hislopi* Lydekker, 1885 (ISI R43), detail of snout portion in dorsal view. *Abbreviations:* na, nasal; nar, naris; nr, narial rim; pmx, premaxilla; smx, ‘septomaxilla.’ [formatted for column width]

FIG. 11. Referred skull of *Parasuchus hislopi* Lydekker, 1885 (ISI R43), detail of snout portion in left lateral view. *Abbreviations:* afen, antorbital fenestra; afos, antorbital fossa; mx, maxilla; na, nasal; nar, naris; nr, narial rim; pmx, premaxilla; smx, ‘septomaxilla.’ [formatted for page width]

FIG. 12. Referred skull of *Parasuchus hislopi* Lydekker, 1885 (ISI R43), detail of snout portion in ventral view, partially restored in plaster (white). *Abbreviations:* cho, choana; ipf, interpremaxillary fossa; mx, maxilla; pal, palatine; pmx, premaxilla. [formatted for page width]

FIG. 13. Referred skull of *Parasuchus hislopi* Lydekker, 1885 (ISI R44) from the Tiki Formation. A, dorsal view. B, ventral view. C, right lateral view. [formatted for column width]

FIG. 14. Comparison between *Parasuchus* species. A–D in right lateral view, E–G in dorsal view (anterior is right). A and F, neotype skull of *Parasuchus hislopi* Lydekker, 1885 (ISI R42). B and E, holotype skull of *Parasuchus angustifrons* (Kuhn, 1936) (BSPG 1931 X 502). C, referred skull of *Parasuchus bransoni* (Williston, 1904) (TMM 31100-101). D, holotype skull of *Parasuchus bransoni* (Williston, 1904) (FMNH UC 632). G, holotype skull of *Parasuchus magnoculus* (Dutuit, 1977) (MNHN-ALM1). Note identical shape of the narial eminence in C and D (tall, triangular, nares facing anteriorly), autapomorphic for *P. bransoni*. *Abbreviation:* nd, nasal depression. [formatted for page width]

FIG. 15. Strict consensus tree of phytosaur relationships based on the results of the phylogenetic analysis. Named nodes indicated with black circles. Numbers above nodes represent bootstrap values, numbers below represent Bremer support values. [formatted for page width]

TABLE 1. Upper Gondwana formations of Pranhita-Godavari and Rewa basins and the vertebrate fauna of the Maleri and Tiki formations (modified after Bandyopadhyay 2011; Novas *et al.* 2011; Mukherjee *et al.* 2012; Mukherjee and Ray 2014; Ray 2015). Hutchinson *et al.* (2012) argued that *Tikiguania* was a Cenozoic agamid reworked into Triassic sediments; it is listed here for sake of completeness.

Basin		Pranhita-Godavari Basin		Rewa Basin		Vertebrate fauna of Maleri Formation	Vertebrate fauna of Tiki Formation	
Age								
Jurassic		Middle 175.6±2.0	Kota		Parsora		Upper <i>Xenacanthus indicus</i> <i>Ceratodus nageswari</i> <i>Compsocerops cosgriffi</i> <i>Kuttycephalus triangularis</i> <i>Angistorhinus</i> sp. cf. <i>Leptosuchus</i> <i>Aetosauria</i> indet. <i>Nambalia roychowdhurii</i> <i>Jaklapallisaurus asymmetrica</i> cf. <i>Ischigualastia</i>	
		Lower 199.6±1.5						
Triassic	Upper	Rhaetian 203.6±2.0	Dharmaram					
		Norian 216.5±2.0				Maleri		
		Carnian 228±2.0	Lower	Tiki				
	Middle	Ladinian 237±2.0	Bhimaram			Karki		
		Anisian 245±1.5						
Lower	Olenekian	Kamthi		Pali				
						Lower <i>Xenacanthus indicus</i> <i>Ptychoceratodus hislopianus</i> <i>Ptychoceratodus virapa</i> <i>Metoposaurus maleriensis</i> <i>Hyperodapedon huxleyi</i> <i>?Malerisaurus robinsonae</i> <i>Parasuchus hislopi</i> cf. <i>Angistorhinus</i> cf. <i>Typothorax</i> <i>Alwalkeria maleriensis</i> <i>Exaeretodon statisticae</i> <i>Deccanodon maleriensis</i>	 <i>Ceratodus</i> sp. <i>Metoposaurus maleriensis</i> <i>Hyperodapedon tikiensis</i> <i>Tikiguania estesi</i> <i>Parasuchus hislopi</i> <i>Tikisuchus romeri</i> <i>Ruberodon roychowdhurii</i> <i>Rewaconodon tikiensis</i> <i>Gondwanadon tapani</i> <i>Tikitherium copei</i>	

TABLE 2. Taxonomic history of ‘*Paleorhinus*-grade’ phytosaur species.

¹Lucas *et al.* (2007) did not formalize new combinations, but in the text they state that they consider all taxa included in *Paleorhinus* in Hunt and Lucas (1991) to pertain to *Parasuchus*.

²Hunt and Lucas (1991) considered the type material of *P. hislopi* to be generically indeterminate, although they still recommended use of the species name *Paleorhinus hislopi* for ISI R42 and R43.

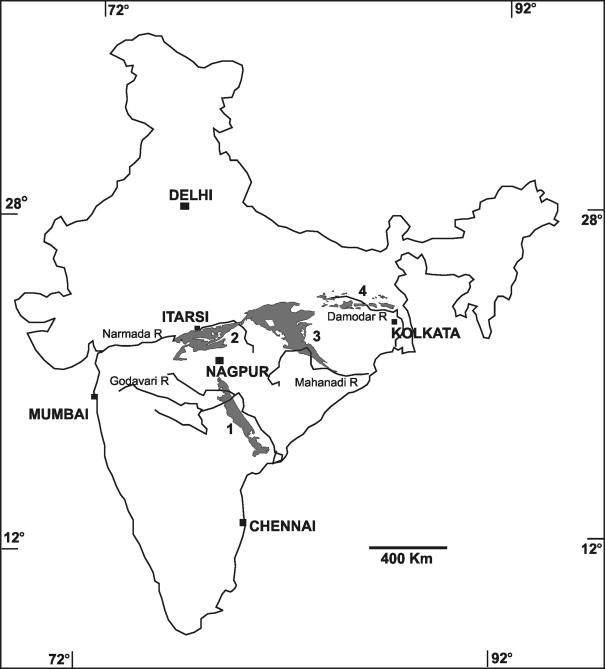
³Long and Murry (1995) suspected that all the ‘*Paleorhinus*’ species from the Ebrach quarry were synonymous, in which case the senior name would be *Paleorhinus broilii*, but were unable to confirm this hypothesis, not having examined the material personally.

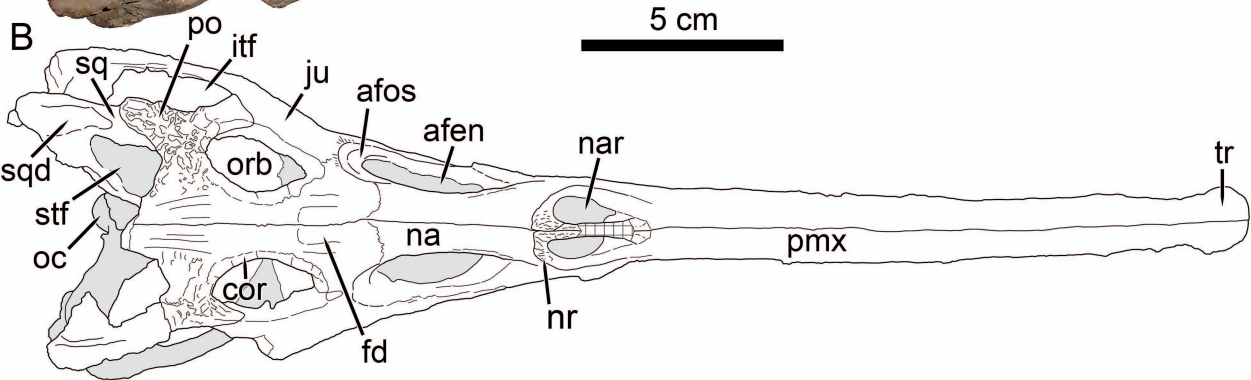
Original description	Gregory (1962)	Hunt & Lucas (1991)	Long & Murry (1995)	Lucas <i>et al.</i> (2007) ¹	Stocker & Butler (2013)	This study
<i>Parasuchus hislopi</i> Lydekker, 1885	Phytosauria indet.	Phytosauria indet. ²	Phytosauria indet.	<i>Parasuchus hislopi</i>	<i>Parasuchus hislopi</i>	<i>Parasuchus hislopi</i>
<i>Paleorhinus bransoni</i> Williston, 1904	<i>Paleorhinus bransoni</i>	<i>Paleorhinus bransoni</i>	<i>Paleorhinus bransoni</i>	<i>Parasuchus bransoni</i>	<i>Paleorhinus bransoni</i>	<i>Parasuchus bransoni</i>
<i>Mesorhinus fraasi</i> Jaekel, 1910	? <i>Paleorhinus fraasi</i>	<i>Paleorhinus</i> sp.	unassigned	<i>Parasuchus</i> sp.	uncertain	uncertain
<i>Promystriosuchus ehlersi</i> Case, 1922	<i>Paleorhinus ehlersi</i>	<i>Paleorhinus bransoni</i>	<i>Paleorhinus ehlersi</i>	<i>Parasuchus bransoni</i>	uncertain	uncertain
<i>Paleorhinus parvus</i> Mehl, 1928	<i>Paleorhinus parvus</i>	<i>Paleorhinus bransoni</i>	unassigned	<i>Parasuchus bransoni</i>	‘ <i>Paleorhinus</i> ’ <i>parvus</i>	‘ <i>Paleorhinus</i> ’ <i>parvus</i>
<i>Francosuchus broilii</i> Kuhn, 1933	<i>Paleorhinus broilii</i>	<i>Paleorhinus</i> sp.	uncertain ³	<i>Parasuchus</i> sp.	Phytosauria indet.	Phytosauria indet.
<i>Francosuchus latus</i> Kuhn, 1933	<i>Paleorhinus broilii</i>	<i>Paleorhinus</i> sp.	uncertain ³	<i>Parasuchus</i> sp.	Phytosauria indet.	Phytosauria indet.
<i>Ebrachosuchus neukami</i> Kuhn, 1936	<i>Paleorhinus neukami</i>	<i>Paleorhinus neukami</i>	<i>Paleorhinus neukami</i> ³	<i>Parasuchus neukami</i>	<i>Ebrachosuchus neukami</i>	<i>Ebrachosuchus neukami</i>
<i>Francosuchus angustifrons</i> Kuhn, 1936	<i>Paleorhinus broilii</i>	<i>Paleorhinus</i> sp.	uncertain ³	<i>Parasuchus</i> sp.	<i>Paleorhinus angustifrons</i>	<i>Parasuchus angustifrons</i>

<i>Paleorhinus scurriensis</i> Langston, 1949	<i>Paleorhinus scurriensis</i>	<i>Paleorhinus bransoni</i>	<i>Paleorhinus bransoni</i>	<i>Parasuchus bransoni</i>	<i>'Paleorhinus' scurriensis</i>	<i>Wannia scurriensis</i>
<i>Paleorhinus magnoculus</i> Dutuit, 1977	—	<i>Paleorhinus magnoculus</i>	<i>Arganarhinus magnoculus</i>	<i>Parasuchus sp.</i>	<i>'Paleorhinus' magnoculus</i>	<i>Parasuchus magnoculus</i>
<i>Paleorhinus sawini</i> Long & Murry, 1995	—	—	<i>Paleorhinus sawini</i>	unassigned	<i>'Paleorhinus' sawini</i>	<i>'Paleorhinus' sawini</i>

TABLE 3. Summary of higher-level taxonomic changes in Phytosauria made between the most recent review of the clade (Stocker and Butler 2013) and this study.

Stocker & Butler (2013)	Present study
Phytosauria Jaeger, 1828 (stem): <i>Rutiodon carolinensis</i> and all taxa more closely related to it than <i>Aetosaurus ferratus</i> , <i>Rauisuchus tiradentes</i> , <i>Prestosuchus chiniquensis</i> , <i>Ornithosuchus woodwardi</i> , or <i>Crocodylus niloticus</i>	Phytosauria Jaeger, 1828 (stem): unchanged
(no name given for this node)	Parasuchidae Lydekker, 1885 (node): <i>Wannia scurriensis</i> , <i>Parasuchus hislopi</i> , <i>Mystriosuchus planirostris</i> , and all descendants of their most recent common ancestor
Phytosauridae Jaeger, 1828 (node): <i>Angistorhinus</i> , <i>Leptosuchus studei</i> , <i>Mystriosuchus westphali</i> , and all descendants of their most recent common ancestor	Mystriosuchinae Huene, 1915 (node): <i>Mystriosuchus planirostris</i> , <i>Angistorhinus grandis</i> , and all descendants of their most recent common ancestor
Leptosuchomorpha Stocker, 2010 (node): <i>Leptosuchus studei</i> , <i>Machaeroprotopus pristinus</i> , and all descendants of their most recent common ancestor	Leptosuchomorpha Stocker, 2010 (node): unchanged
Pseudopalatinae Long & Murry, 1995 (node): <i>Nicrosaurus kapffi</i> , <i>Mystriosuchus westphali</i> , <i>Machaeroprotopus pristinus</i> , <i>Redondasaurus gregorii</i> , and all descendants of their most recent common ancestor	Mystriosuchini Huene, 1915 (node): <i>Nicrosaurus kapffi</i> , <i>Mystriosuchus planirostris</i> , <i>Machaeroprotopus buceros</i> , and all descendants of their most recent common ancestor



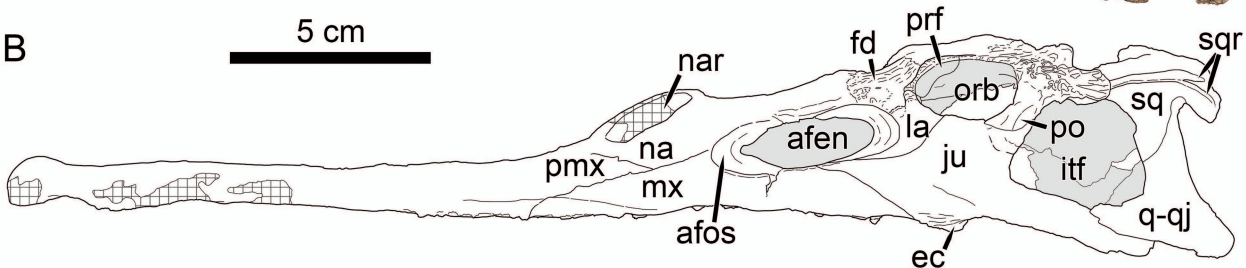


A



B

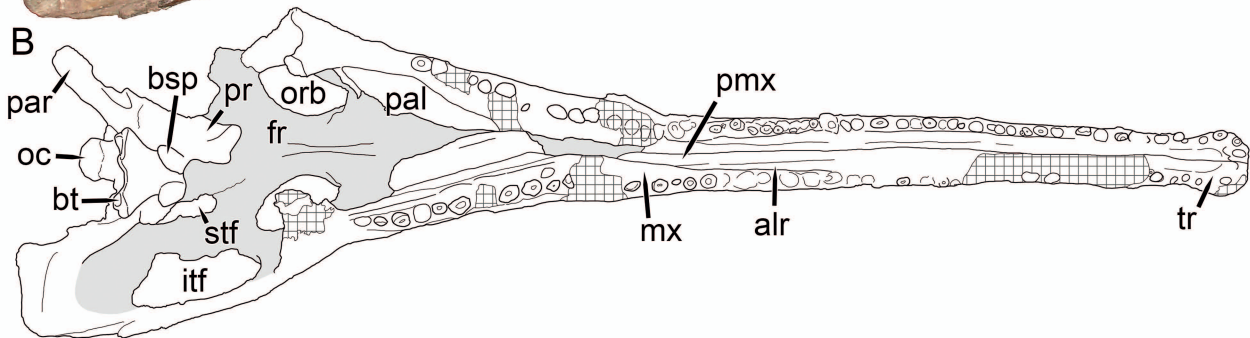
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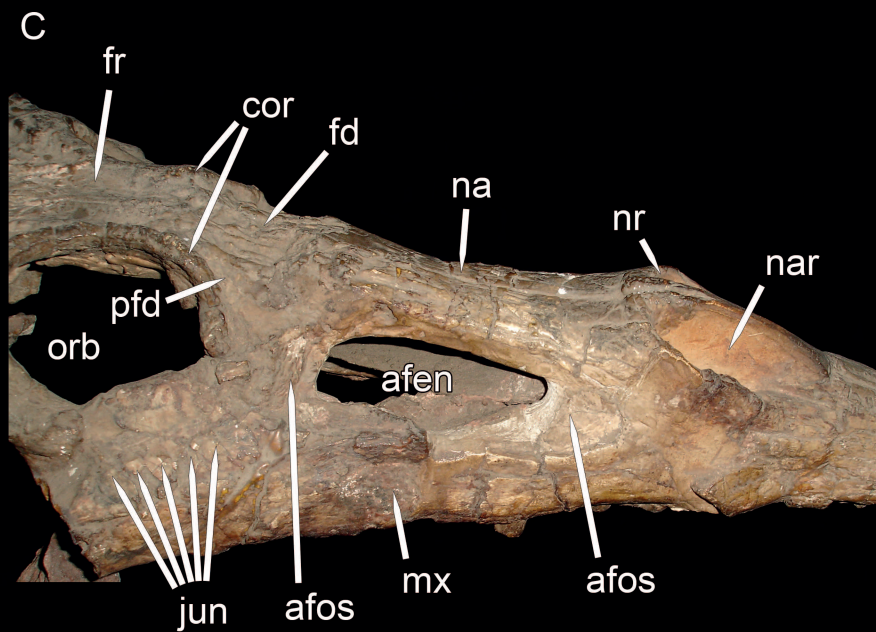
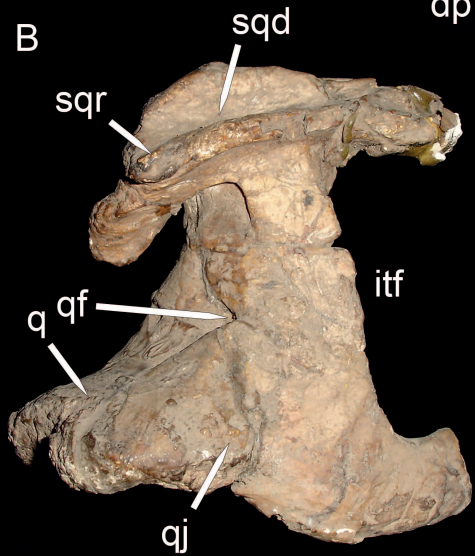


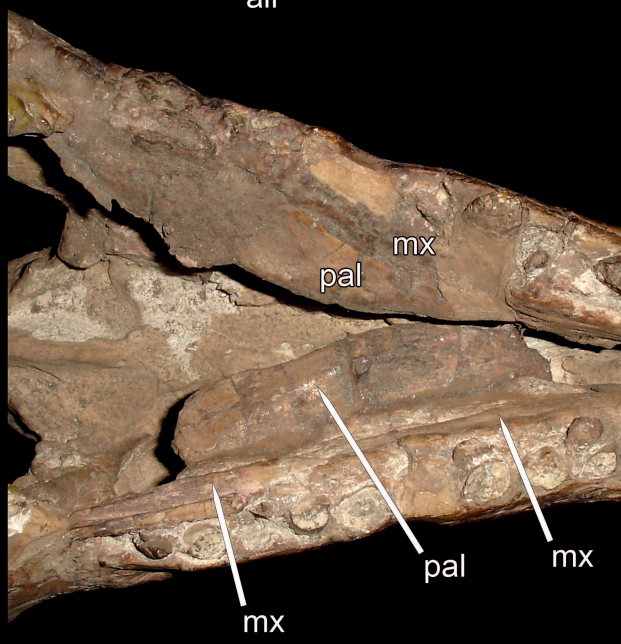
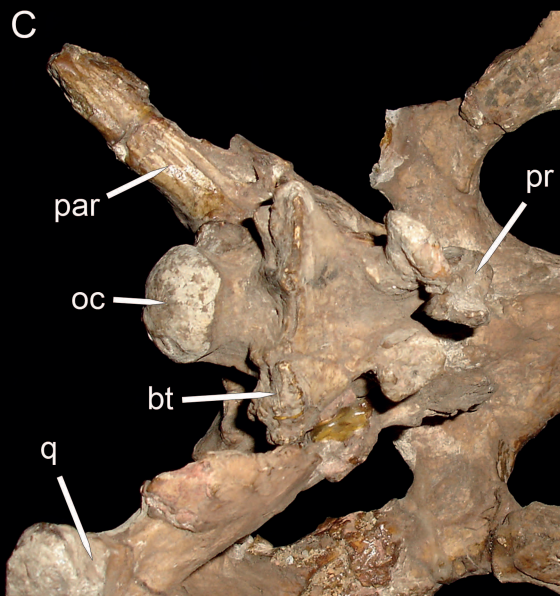
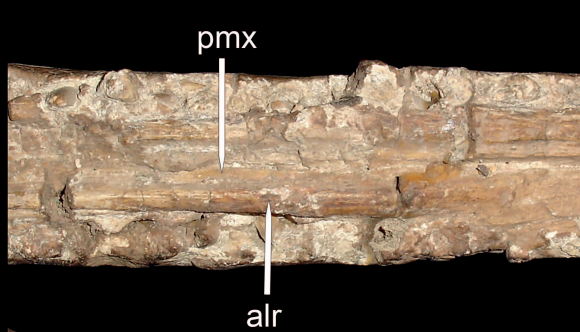
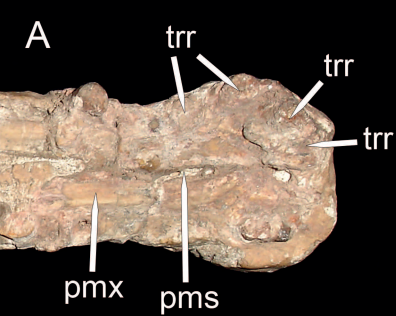
A

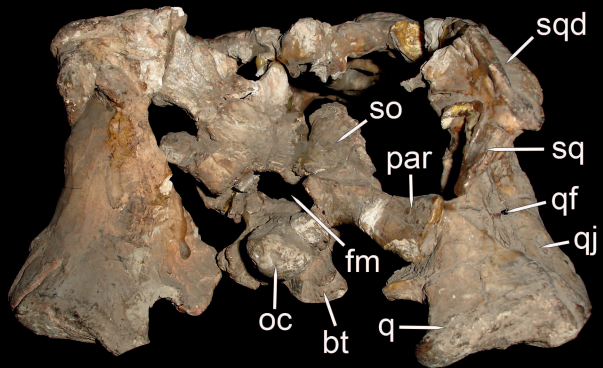


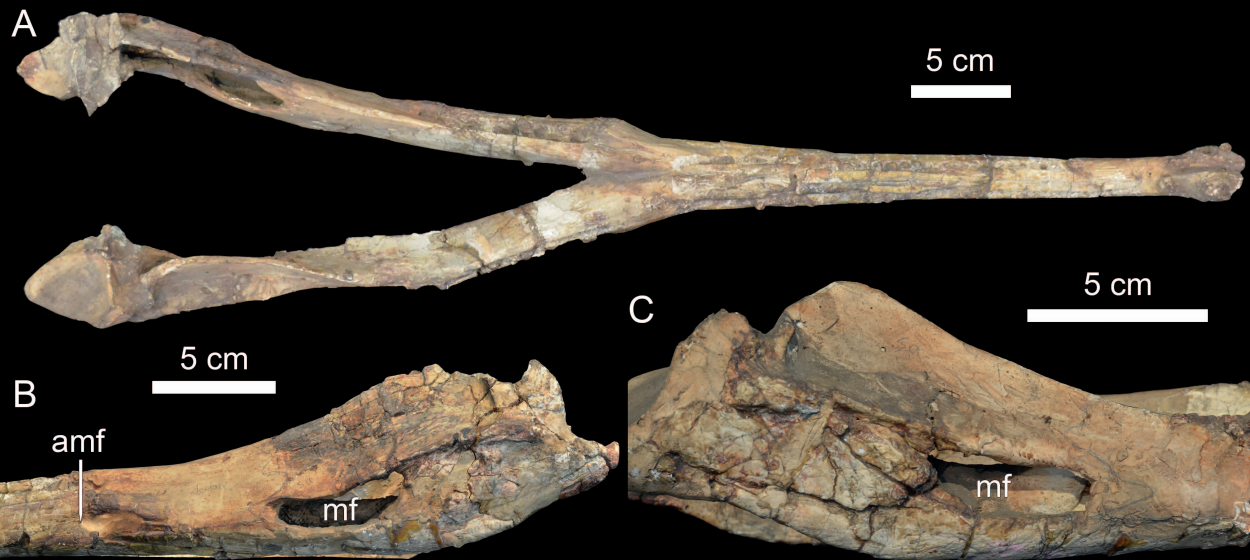
B

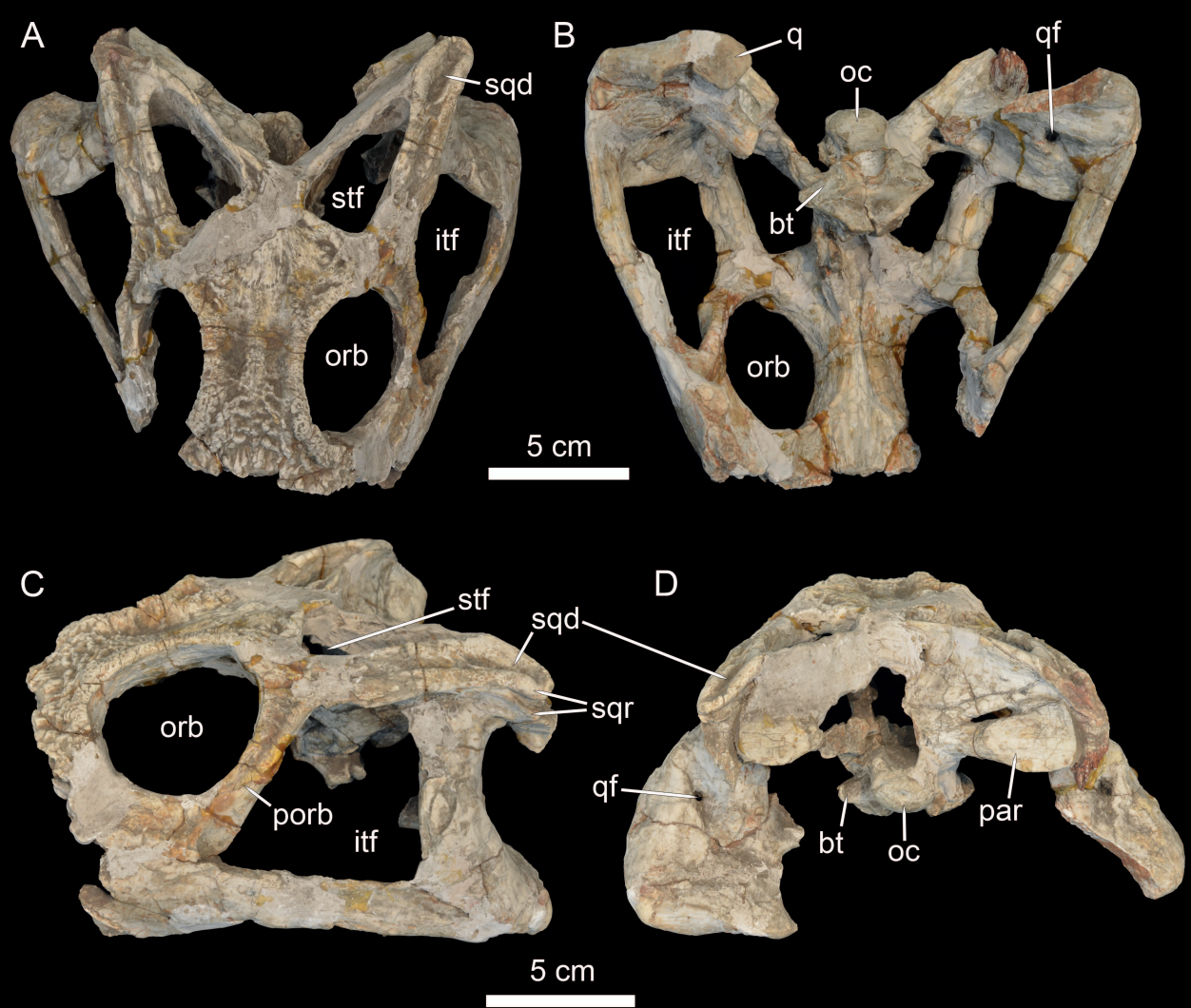












5 cm



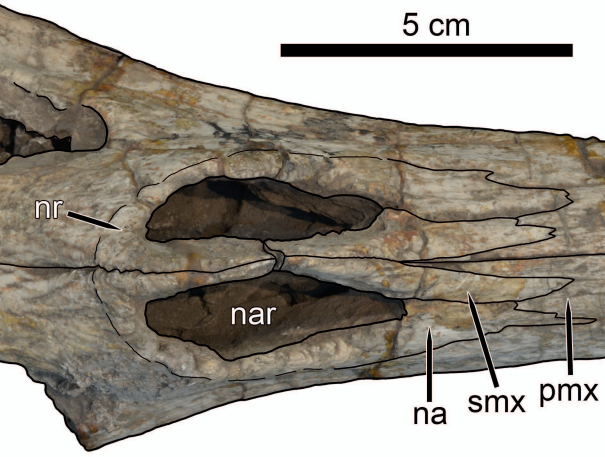
nr

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smx

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5 cm

smx

nar

nr

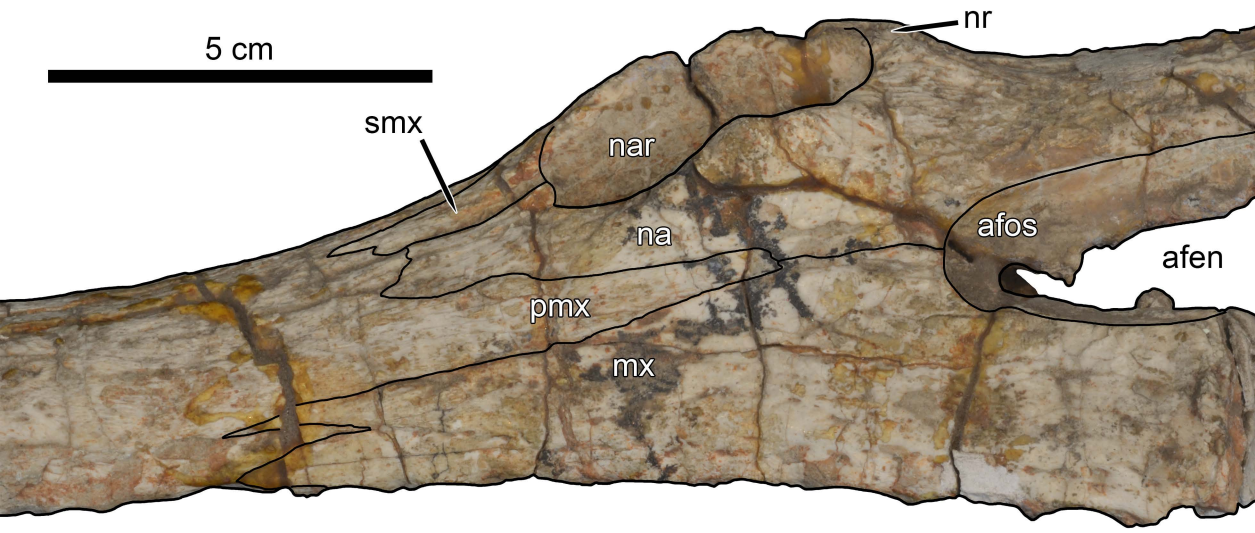
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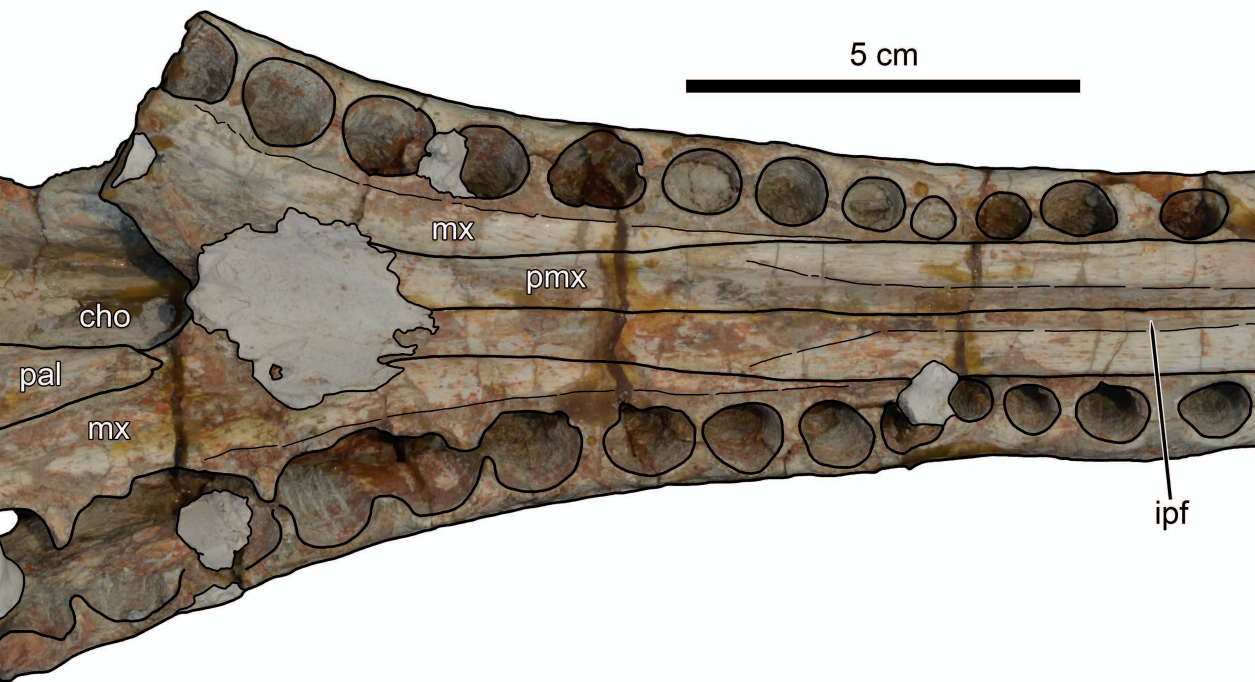
afos

afen

pmx

mx





A



B



5 cm



C





A



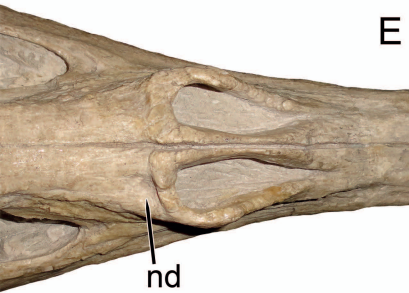
B



C



D



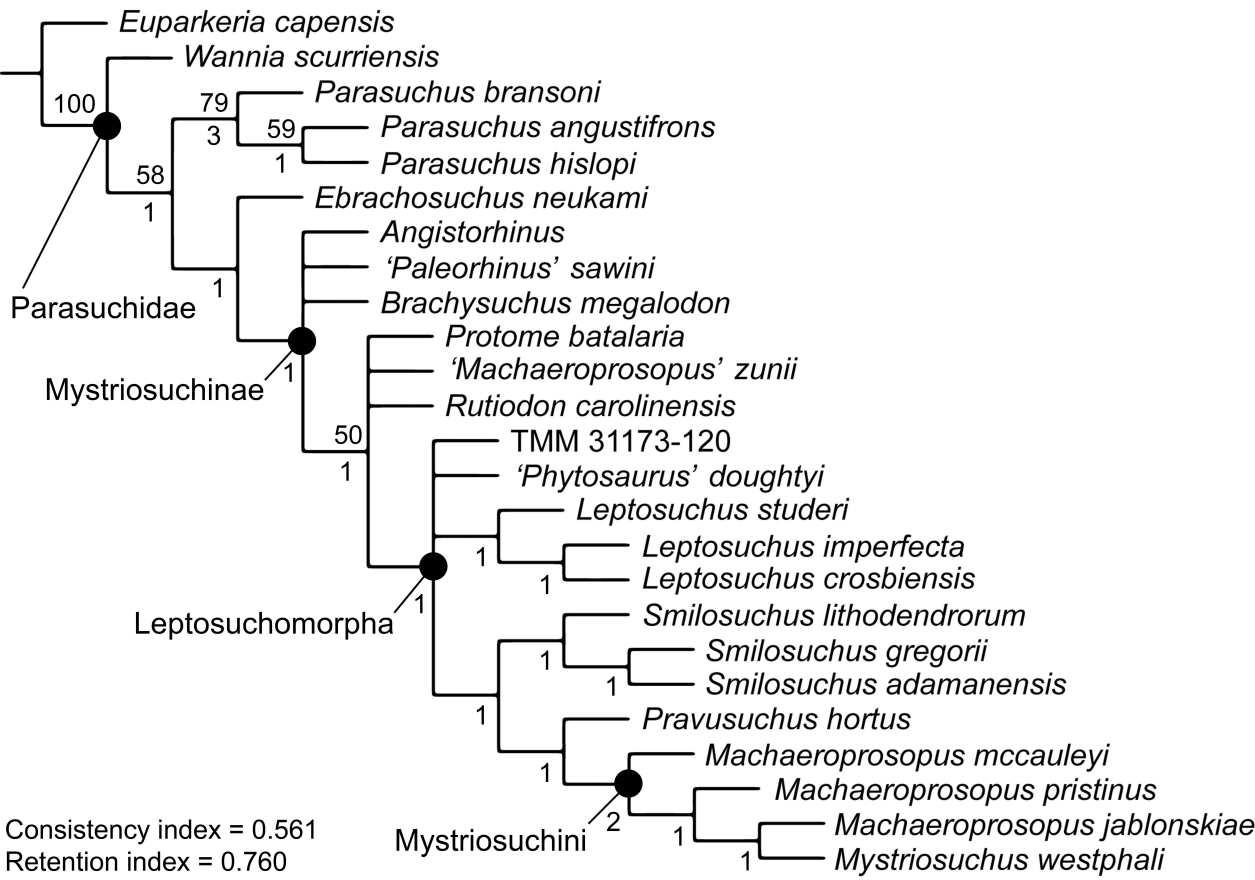
E



F



G



APPENDIX

New characters

Numbering continues from the character list of Butler *et al.* (2014):

47. Broad median depression on dorsal surface of frontals, near border with nasals: (0) absent; (1) present. This depression extends across the anterior portion of the frontals, anterior to the orbits, in species of *Parasuchus* (e.g. Fig. 2B). It is separate from the crescentic prefrontal (preorbital) depressions.

48. Posterolateral margins of nares swollen and rugose, creating a distinct ‘narial rim’: (0) absent; (1) present. The narial region is raised in most phytosaurs, but the morphology of this feature varies widely in the group. In *Parasuchus bransoni* and most other phytosaurs, the naris is situated on a raised eminence of varying rugosity that gradually slopes down towards the flatter posterior portion of the nasal. In *Parasuchus angustifrons*, however, the posterolateral margin of the naris forms a discrete, swollen ‘narial rim’ with a distinct break in slope from the surrounding nasal (see Fig. 14E). A similar morphology is present in *P. hislopi* (Figs 10, 14F), although slightly less pronounced (which may be due to overpreparation).

Data matrix

<i>Euparkeria capensis</i>	00001000000??0000??000?0000?0?000000000?00000000
<i>Wannia scurriensis</i>	1101???1?0?10?1?????000001?0??000?0??00001?????
<i>Parasuchus bransoni</i>	111?11?10011022010?01030001?0?100000001001?10010
<i>Parasuchus angustifrons</i>	111011??00?10?2?????01030001?0?10000?0?1000110011
<i>Ebrachosuchus neukami</i>	112?111??0?1032010?01000001?0?0000020?1000101100
<i>‘Paleorhinus’ sawini</i>	112??0?101???2?010?01000001?0?1001031?101??0?00?
<i>Brachysuchus megalodon</i>	12?110110111012010????01110100?10011?11????1?01000
<i>Angistorhinus</i>	122??0110011012010?0101010100?10011??0???1?01100

<i>Rutiodon carolinensis</i>	122??111001??2?010?01?1120000011000??0???1101110
<i>'Phytosaurus' doughtyi</i>	1?2??1?????????????0101220010111?001???????????
<i>Leptosuchus crosbiensis</i>	1221?1110120?12001000012200101110002?1???1?00100
<i>Leptosuchus imperfecta</i>	12???11?0?2?????010???1?2?0?0??1?00??1??????0???
<i>Leptosuchus studeri</i>	12211111012001210100001220010011000211???1?01100
<i>Smilosuchus adamanensis</i>	1230011101210120010?111121000011100?012111201100
<i>Smilosuchus lithodendrorum</i>	12?0?111012??12001100?1220000011100??1???1201???
<i>'Machaeroprotopus' zunii</i>	1?2??1?????????????01011210001?1?001??2????0???0
<i>Smilosuchus gregorii</i>	123001111120012001201111210000111001?12??1201100
<i>Pravusuchus hortus</i>	123001110120112001000112210111111001112111?01?00
<i>Protome batalaria</i>	1????1110?????2010?01112210001?1?00??121??????0?
TMM 31173-120	122??111002001200100001221010111100111211120110?
<i>Machaeroprotopus jablonskiae</i>	1????1?????????????01??10101?0?22000??211????100
<i>Machaeroprotopus mccauleyi</i>	123??1121120012001110222110011122001202?112?11??
<i>Machaeroprotopus pristinus</i>	12300112101002201???1222110111122001202111201100
<i>Mystriosuchus westphali</i>	123001121111022111?00200010?1012100?00???1?01100
<i>Parasuchus hislopi</i>	11101101?01??22010?01030001?0?100????010???10011